

USING VOCAL INDIVIDUALITY TO MONITOR QUEEN CHARLOTTE SAW-WHET OWLS (*AEGOLIUS ACADICUS BROOKSI*)

CARMEN I. HOLSCHUH¹ AND KEN A. OTTER

Ecosystem Science & Management Program, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9 Canada

ABSTRACT.—Our goal was to assess whether male Northern Saw-whet Owls (*Aegolius acadicus brooksi*) in the Queen Charlotte Islands have sufficient variation in the notes of their territorial/ advertisement call to identify individuals within and between breeding seasons. Recordings of calling bouts were collected from 24 sites over the 2-yr study period and analyzed using discriminant function analysis. Using recordings of eight sites in 2002 and 16 sites in 2003, we correctly identified novel notes collected during a single recording session for 69% and 75% of the samples, respectively. Of the 13 sites for which we had multiple nights of recordings, 73% of notes measured from a novel night were classified to the correct site. The data also suggested that vocal individuality can be used to monitor site fidelity and rates of territory turnover of male owls across years, as correct classification of males re-occupying specific sites across years (>60%) was greater than rates of random classification (\bar{x} = 3.3%, maximum = 19%). Vocal individuality, thus, appears to have promise as a useful tool for monitoring and studying life history parameters of Northern Saw-whet Owls both within and between years.

KEY WORDS: *Northern Saw-whet Owl*; *Aegolius acadicus brooksi*; *site fidelity*; *vocal individuality*.

USO DE LA INDIVIDUALIDAD VOCAL PARA MONITOREAR BÚHOS *AEGOLIUS ACADICUS BROOKSI* EN LAS ISLAS QUEEN CHARLOTTE

RESUMEN.—Nuestro objetivo fue determinar si los machos de *Aegolius acadicus brooksi* de las islas Queen Charlotte presentan suficiente variación en las notas de sus llamados para permitir la identificación de individuos dentro de una época reproductiva y entre épocas reproductivas. Durante un período de dos años, recolectamos grabaciones de vocalizaciones en un total de 24 sitios y las sometimos a análisis discriminantes. Usando grabaciones de ocho sitios en 2002 y de 16 sitios en 2003, identificamos correctamente las notas distintas obtenidas durante una sola sesión de grabación en el 69% y 75% de las muestras, respectivamente. En los 13 sitios para los que teníamos grabaciones hechas durante varias noches, el 73% de las notas medidas en grabaciones de una noche distinta fueron clasificadas correctamente de acuerdo al sitio. Los datos también sugirieron que la individualidad vocal puede emplearse para monitorear la fidelidad al sitio y las tasas de recambio de los territorios de los machos a través de los años, ya que la clasificación correcta de los machos que ocuparon sitios específicos repetidamente en distintos años (>60%) fue mayor que las tasas de clasificación aleatoria (\bar{x} = 3.3%, máximo = 19%). Así, la individualidad vocal parece ser una herramienta promisoriosa para estudiar parámetros de la historia de vida de *A. a. brooksi* tanto en un año como entre años.

[Traducción del equipo editorial]

Avian studies that examine life-history parameters of focal species often require investigators to differentiate among individuals in a population; this is usually accomplished via the application of colored leg bands or radiotelemetry transmitters (Bibby et al. 2000). However, when working on cryptic species, the utility of visual identifiers, such

as leg bands, decreases. Similarly, the invasive nature of radiotelemetry (involving potentially multiple captures of the bird as well as the added mass imposed by the transmitters) may be deemed counterproductive in sensitive species (e.g., Foster et al. 1992). Thus, any cues that study animals inherently possess that distinguish them individually should be explored as a noninvasive method of study. One such cue, vocal individuality in birds, has recently gained popularity as a technique to study visually-cryptic species. Numerous species

¹ Corresponding author's present address: CIH Environmental Consulting, #3-2506 Prior Street, Victoria, BC V8T 3X6 Canada; Email address: holschuh@telus.net

have now been shown to possess sufficient variation in their vocalizations to allow individual identification, including: Eurasian Pygmy Owls (*Glaucidium passerinum*; Galeotti et al. 1993), European Nightjars (*Caprimulgus europaeus*; Reebeck et al. 2001), Great Bitterns (*Botaurus stellaris*; McGregor and Byle 1992), Tawny Owls (*Strix aluco*; Galeotti and Pavan 1991), Bald Eagles (*Haliaeetus leucocephalus*; Eakle et al. 1989), Corncrakes (*Crex crex*; Peake et al. 1998) and Northern Saw-whet Owls (*Aegolius acadicus*; Otter 1996).

An ability to identify male owls accurately within years can yield information about population size, by increasing census accuracy (e.g., Gilbert et al. 1994, Peake and McGregor 2001), and site-specific territory turnovers. Conversely, across year comparisons using vocal characteristics can also indicate site fidelity and between-year territory turnover (e.g., Galeotti and Sacchi 2001, Delpont et al. 2002). For both types of studies, analysis requires not only being able to distinguish between individuals based solely on their vocalizations, but also to classify correctly, and hence recognize, known individuals (McGregor et al. 2000). In this study, we determined the feasibility of monitoring individual male saw-whet owls using their vocalizations, within and between nights during a single year and between years, to determine levels of site fidelity and territory turnover.

There are two distinct subspecies of Northern Saw-whet Owl in North America; *Aegolius acadicus acadicus* occupies most of North America, while *A. a. brooksi* is isolated on an archipelago in northwestern British Columbia, the Queen Charlotte Islands. *A. a. acadicus* is known to be partially migratory and displays low levels of site fidelity and, hence, high territory turnover between years (Cannings 1993). Conversely, *A. a. brooksi* is nonmigratory, yet little is known about other differences in life history of this subspecies, such as prevalence of site fidelity and rates of turnover. The nocturnal nature of these owls coupled with difficult field conditions, makes monitoring individual owls by traditional means, such as banding or color marking, difficult. However, males are highly vocal during the pre-nesting period (Cannings 1993), making male Queen Charlotte Islands saw-whet owls well suited for monitoring via vocal-individuality techniques.

STUDY AREA

Saw-whet owl recordings were collected in the Queen Charlotte Islands of northwestern British Columbia, Can-

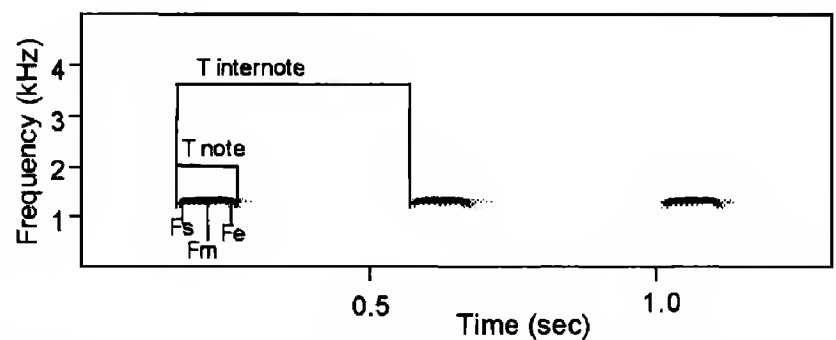


Figure 1. Sonogram of saw-whet owl male advertisement call, illustrating measures taken. Fs, Fm, and Fe refer to measures of frequency at peak amplitude taken from spectral slices at 10%, 50%, and 90% of the note's duration, respectively. Temporal measures were the length of the note (T note) and the internote length (T internote), referring to the time from the start of one note to the start of the next note.

ada (53°N, 131°W). This area is a coastal temperate rainforest with a cool mesothermal climate (cool summers and mild winters) with annual precipitation exceeding 130 cm (Environment Canada). The most common tree species are western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), yellow cedar (*Chamaecyparis nootkatensis*), mountain hemlock (*Tsuga mertensiana*), shore pine (*Pinus contorta* var. *contorta*), and red alder (*Alnus rubra*). The research, with exception of one site, focused on the southern half of Graham Island, the largest island in the archipelago. Parts of the study area have been extensively modified by logging, creating a patchwork of remnant mature and old forest among regenerating stands.

METHODS

We collected recordings of vocal male *A. a. brooksi* during the pre-nesting period (March–May) of 2002 and 2003 within the first 5 hr after sunset. Calls of owls were induced using a 1-min recording of typical saw-whet owl advertisement calling, which is a series of monotonous notes (Fig. 1) repeated at a rate of ca. 2/sec (Cannings 1993) broadcast through a portable CD player and amplified powerhorn (RadioShack 32-2037). All calling activity was recorded using either Sennheiser MKH 70 or ME 67 directional, shotgun microphones (Sennheiser Electronic GmbH & Co. KG, Wedemark, Germany) in combination with Marantz PMD 430 tape recorders (Nihon Marantz Kabushiki Kaisha, Tokyo, Japan). Recordings were restricted to nights with little or no precipitation and low winds. We attempted to approach vocal birds as closely as possible to obtain high-quality recordings, although the structure of the landscape often restricted our approach. Most recordings were made within 100 m of individual birds, with a range up to 300 m in some cases. Distances to the bird were estimated in the field by compass triangulation on the calling owl in addition to estimating direct-line distance. Considering that unobstructed saw-whet owl advertisement vocalizations can travel as far as 1000 m (Cannings 1993) and that the frequency and structural characteristics of this call appear nearly optimal for minimizing degradation in dense

habitat (Wiley and Richards 1982), using recordings collected at a range of up to 300 m should still allow standardized measures to be taken on the individual call notes. When possible, we obtained recordings that minimized environmental background noise (e.g., stream noise, ocean surf). Once a site was deemed occupied, it was visited a minimum of once per wk for the rest of the season in order to monitor the activity and to obtain repeat-recordings of the males.

In total, we recorded calling male saw-whet owls from at least one night at 24 different sites, eight during 2002 and 16 during 2003. Logistics suggested we were recording the same male owls at a particular site, as (1) densities of owls were generally very low due to the fragmented nature of the habitat, and thus, in most cases, it was unlikely there was a second adjacent territory if the focal male had shifted call posts; (2) when there were multiple territories at higher density, simultaneous calling allowed us to identify the males; and (3) the birds were consistent in their calling location, generally calling from within 150 m of previous detection locations. This justification parallels past studies with similar objectives (Galeotti and Pavan 1991, Galeotti et al. 1993, Galeotti and Sacchi 2001). To confirm this assumption, in 2003 we fitted a subset of three male saw-whet owls with small (0.5 g, 3-wk battery life) tail-mount radiotransmitters (Model LB-2, Holohil Electronics, Carp, Ontario, Canada), thereby assuring us that we were recording the same male over multiple nights.

Sonographic Analysis. For each site, we measured a minimum of 20 representative notes of advertisement calling if we only had a single recording session, and up to 56 notes if we had multiple recording sessions, leading to a mean of 35.1 ± 11.2 (SD) notes measured per site. We had collected a mean of 2.2 ± 1.2 recordings per site (range = 1–5). When first screening the recordings, we saved sections of calling that were of high quality (minimal background noise and closest possible proximity to the bird). From those saved files, we randomly chose notes to analyze. Because recordings came in response to a series of 1-min playbacks of the advertisement call, we analyzed only the typical advertisement call and avoided measuring notes given during the more rapid and quiet call that some males seem to include between advertisement calling bouts when highly agitated (also called “introductory notes” [Otter 1996]).

All notes were analyzed using Avisoft SAS Lab Pro 3.8 (Specht 2000). The temporal measures taken were note length (T-note) and internote length (T-internote), which were measured on the waveform screen at a resolution of 2.9 msec. As the frequency range of male saw-whet owl advertisement calls were between 1100–1350 Hz, we filtered out all noise below 900 Hz and above 1500 Hz to focus in on the bird’s signal itself. We defined note length as being from the start of the note at which point the amplitude first begins to increase to the end of the note at which point the amplitude is at one third of its maximum (Fig. 1). This technique was used to account for any differences in the degradation of the notes and to reduce measuring reverberation noise as being part of the note length. This allowed us to measure notes from calls collected at variable distances (25–300 m) from birds without fear of including signal degradation into

the temporal variation between males. The internote length spans from the start of the focal note to the start of the following note. The frequency parameters we measured were the frequency at the beginning (F_s = spectral slice at point 10% into note, as defined by temporal measures), middle (F_m = point at 50% of note length), and end (F_e = point at 90% of note length) of the note. We measured frequency parameters at a frequency resolution of 20 Hz, a temporal resolution of 2.9 ms, and a bandwidth of 56 Hz.

Data Analysis and Individual Recognition. We ran preliminary statistics to assess the variability within each of the five parameters used to classify calls (Galeotti and Sacchi 2001). Analysis of variance (ANOVA) tests for each of the variables, using site identity as the grouping factor, allowed us to measure whether there were appreciable differences in the notes of individual birds at each of the variables. To classify males successfully, it is necessary for the variation in the individual variables to be less within individual sites than the variation between sites. We confirmed this by calculating coefficients of variation of each call measured across all sites (mean across the population), and compared these to mean coefficients of variation within sites (mean within males).

To test the ability to classify individuals correctly based on their vocalizations, we used the general discriminant analysis function (forward stepwise, P to enter/remove = 0.05) in STATISTICA (StatSoft, Inc. 2003). We analyzed calls from a single night of recordings for each of the eight sites from 2002 and 16 sites from 2003 separately to determine levels of correct classification within a single night (i.e., known to be recordings from the same male, as notes were taken from a continuous bout of calling). The discriminant function was built from a learning set of 66% of the calls. A test set contains the remaining calls, which are not used in the discriminant function itself, but are introduced as novel cases to be classified to site by the model. By using this approach of classifying novel notes, the estimation of correct classification rates should be more representative than when using more common analysis techniques in which the same notes that were used to build the discriminant function are later classified (Terry and McGregor 2002).

To test the ability of the model to classify males to the correct sites across nights, we used 13 sites from both years for which we had multiple detections. We used notes that were collected from one night to build a learning set (from which the discriminant function was developed), and notes recorded from a separate night during the same season as a test-set. Using the cross-validation function, we classified test notes to specific sites using the discriminant function built from the learning set. If the classification accuracy for a single male between nights was comparable to within nights (see above analysis), it is likely the same male, whereas if the between night comparison has lower classification success, a territory turnover event may have occurred.

Site Fidelity/Territory Turnover. To determine whether territories were being occupied for both field seasons, we repeatedly revisited all sites during the 2003 field season that had been occupied in 2002. A site was deemed occupied in both years if we found calling activity on any night during the 2003 visits. We monitored occupied sites

Table 1. Parameters characterizing the notes of advertisement/territorial calling of male saw-whet owls. Notes measured for each of 24 males (8 from 2002 and 16 from 2003) were used to derive a coefficient of variation for measured parameters for each male; mean coefficients of variation for individuals (CV ind.) were then calculated. Means, standard deviations (SD), and range (maximum and minimum values) and coefficients of variation across males in the population (CV group) were derived from the mean value of each note parameter across the 24 males (N). F values reflect a comparison between CV group compared to CV individual.

	N	MEAN \pm SD	MINIMUM	MAXIMUM	CV (GROUP)	CV (IND.)	F -RATIO	df	P
T-note	24	112 \pm 13 ms	72 ms	142 ms	12.03	6.64	85	23	<0.001
T-internote	24	431 \pm 64 ms	273 ms	697 ms	14.80	9.47	46	23	<0.001
F (s)	24	1173 \pm 41 Hz	1070 Hz	1310 Hz	3.50	1.37	191	23	<0.001
F (m)	24	1194 \pm 48 Hz	1090 Hz	1350 Hz	3.98	1.41	210	23	<0.001
F (e)	24	1197 \pm 51 Hz	1090 Hz	1370 Hz	4.37	1.49	224	23	<0.001

regularly (1/wk) and attempted to re-record the resident male. For sites with 2 yr of recordings, we ran a discriminant function analysis comparing recordings from the site in either year using the cross-validation function in the general discriminant analysis module. Recordings from 2002 were used as a learning set to develop the discriminant model; with this model, we attempted to classify recordings from the same site in 2003, which constituted the test set. To determine how the model would classify songs from two different males (such as would occur if the resident male differed between years), we also included seven sites from 2002 in the learning set that were not reoccupied in 2003, and randomly paired these with seven different sites (and presumably different males) from 2003. This control set served two functions: (1) it allowed us to determine how frequently calls from two different males would be cross-classified by chance, and (2) by increasing the total number of sites in the learning set, we decreased the probability that our focal sites would be cross-classified by chance alone. If the level of cross-classification of the focal sites was greater than the level of classification among sites with known different individuals (control set), we considered the site to be occupied by the same male. Conversely, if reclassification between years was low and similar to the control set, it suggested that a territorial turnover had occurred.

RESULTS

The coefficients of variation in call measures were significantly greater across males (CV groups) in the population than the mean variation within an individual male (CV ind; Table 1).

Within Year Vocal Individuality. In measuring the ability to correctly classify notes collected within a single recording session, the discriminant function analysis had an 84% ability to classify notes correctly used to build the discriminant function, and a 69% ability to classify novel notes correctly introduced into the analysis (test set) for the eight sites in 2002. In 2003, when 16 sites were used, the discriminant function correctly classified

84% of notes used in the learning set of the discriminant function and 75% of the novel notes used in the test set.

We were able to obtain multiple nights of within-year recordings for 13 males. On average, we analyzed 46 (\pm 9 SD, range 31–56) notes for each of these males. We used a mean of 30 (\pm 9 SD, range = 15–39) of these notes from recordings on a single night as the learning set to create the discriminant function and 15 (\pm 4 SD, range = 9–22) notes from a separate night as the test set to test the discriminant model in cross-validation analysis. We were able to classify notes correctly within the learning set a mean of 79% of the time, while classification of notes from a different night (test set) had a mean of 74% correct classification (Table 2). Correct classification of recordings across different nights from males fitted with radiotransmitters ranged from 38–100%, indicating that there was variation between nights in the note structure of known males.

One site had a disproportionately lower level of correct classification than the others, which may have indicated that a different male took over the territory between the two recordings (separated by 5 wk). When classification accuracy was examined within night, 70% of novel notes introduced into the discriminant analysis were classified correctly, whereas only 7% of notes were classified correctly from a different night.

All variables significantly contributed to the discriminant function (Table 3), although the variables that loaded most heavily on building the function were note length and frequency at the end of the note (indicated by highest F -ratio values). We explored the misclassification of particu-

Table 2. Percent of correct classification of notes in male saw-whet owls with multiple recordings within seasons. The learning set was composed from recordings collected during one or more detections at each site. The test set calls originated from a separate recording session at the same site. Hence, the test set notes were not used in building the discriminant function; they were used instead for testing correct classification of novel notes.

SITE	YEAR	WITHIN NIGHT CLASSIFICATION	BETWEEN NIGHT CLASSIFICATION
1	2002	100	87
2	2002	100	87
3	2002	85	60
4	2002	100	87
5	2003	40	78
6	2003	85	81
7	2003	58	95
8	2003	100	85
9	2003	70	7
10	2003	85	73
11 ^a	2003	100	60
12 ^a	2003	16	100
13 ^a	2003	80	39

^a Males had transmitters that allowed for the confirmation of identity.

lar males by comparing the distances to the nearest neighbor and to the site to which a focal male was most often misclassified. We found that males were usually misclassified not with adjacent sites, but with sites that were significantly further away than mean inter-male spacing ($t = -7.531$, $df = 19$, $P < 0.0001$; Fig. 2).

Site Fidelity and Territory Turnover in Saw-whet Owls. Of the 13 sites from 2002 that we monitored regularly for both field seasons, seven sites were occupied again in 2003, indicating a 53% reoccupancy rate of sites. We were able to collect recordings of sufficient quality at three of these sites to analyze whether the same males were occupying those territories (Fig. 3). By examining the cross-classification rate of control sites, we determined a random cross-classification of calls from two different males averaged 3%, with a maximum of 19%. Two of the three focal sites occupied both years had much greater levels of correct classification (>60%) than this, suggesting that the same male was occupying the sites during both breeding seasons. However, one site had 0% correct classification of notes, indicating a turnover had likely occurred (Table 4).

Table 3. Results of multivariate analysis (Wilks's test) to determine differences between calling males at each of the contributing parameters measured on the notes.

	F-RATIO	df	P
T-note	47.7656	23	<0.0001
T-internote	25.6395	23	<0.00001
F (s)	21.9992	23	<0.00001
F (m)	24.9339	23	<0.00001
F (e)	37.6732	23	<0.00001

DISCUSSION

Our results suggest that male Northern Saw-whet Owls may have sufficient variation in their advertisement calls to allow successful discrimination between individuals within and between nights, and that it may be possible to use this technique to monitor these owls across years. However, some limitations exist that affect the reliability of identifying some males correctly. Inherent variation in male owl advertisement calls of some individuals still present challenges in classifying some males to the correct sites. Further, our study site was characterized by a rugged landscape, which often prevented close approach to vocal owls, thereby sometimes compromising recording quality. Although we took steps to limit measuring reverberation in calls, such degradation could still introduce variability that can result in lowered discriminant ability to identify birds. Also, as it is primarily the male saw-whet owls who employ the advertisement call,

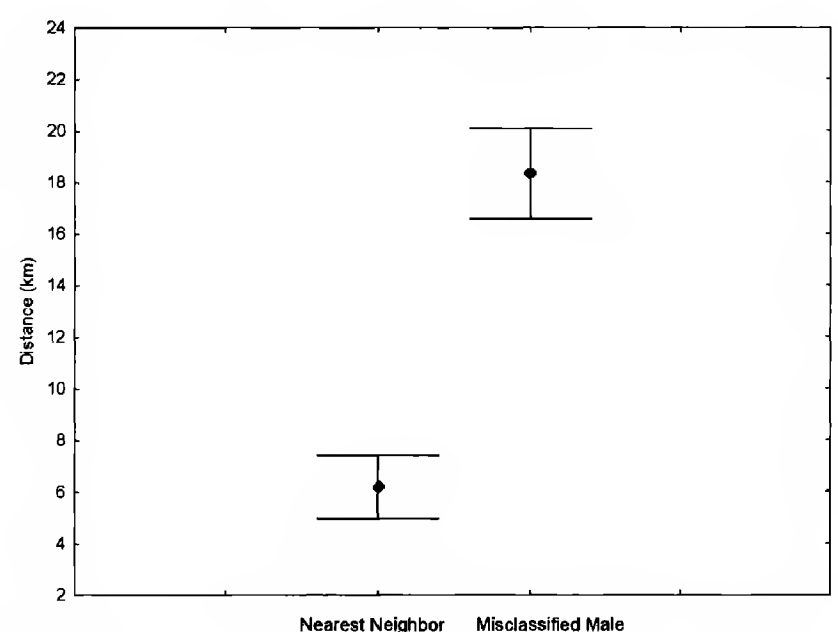


Figure 2. Comparison of mean distances between nearest neighbor to each male saw-whet owl and the mean distance to the site any given site was most often misclassified as ($N = 20$).

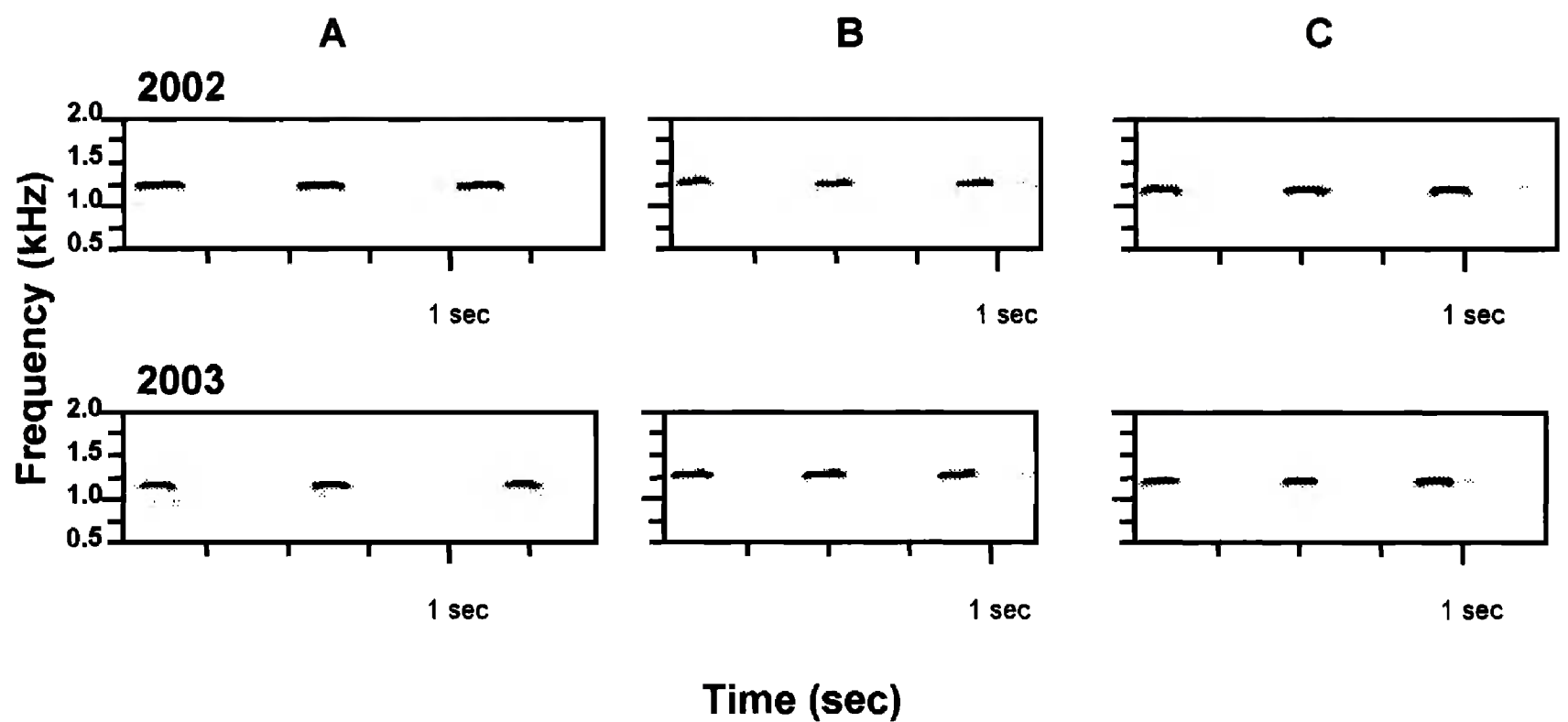


Figure 3. Spectrograms of three male Queen Charlotte saw-whet owls occupying the same sites in 2002 and 2003. Site location is indicated as A, B, or C. Recordings of males occupying the territories in either 2002 (upper spectrogram) or 2003 (lower spectrogram) are shown. Discriminate analysis on vocal characteristics indicated that the same males reoccupied sites B and C across the two years, but discrepancies in vocal signals between years in site A suggest a territorial turnover.

this technique is not as applicable in learning about female territoriality and site fidelity.

Some of the lack of reliability can be overcome by interpreting the results in context of the location of calling males across the landscape. When

the model misclassified males, it usually attributed the note to a male distant from the singer. Neighboring males seem to not converge on similar call patterns, either by overlapping or frequency matching each other in call structure, the converse

Table 4. Classification of novel notes recorded in 2003 (test set) using discriminant functions based on the learning set of recordings collected at sites in 2002. The numbered sites (1–7) refer to control sites, where the test set (2003) recordings were from different males than in the learning set (2002). The lettered sites (A–C) were sites that were occupied both years of the study. The numbers in the matrix refer to the classification of individual notes recorded in 2003 (test set) to individual sites. Of the sites occupied both years, sites B and C appeared to be defended by the same male, whereas site A likely experienced a territory turnover.

SITE	PERCENT CORRECT	NO. NOTES CLASSIFIED	LEARNING SET (2002 RECORDINGS)										
			1	2	3	4	5	6	7	A	B	C	
Test set (2003 recordings)													
1	0.00	38	0		4	16	3				14	1	
2	0.00	32	1	0	5	8				1	12	4	1
3	0.00	24		13	0		7	4					
4	4.26	47	4		27	2	1				13		
5	0.00	30		27			0	3					
6	0.00	15						0			10	5	
7	18.75	48	4			12				9	2	2	19
Control	3.29												
A	0.00	17	1	3				3	5		0	5	
B	64.91	57	5	2	5			5	2		1	37	
C	61.29	31					9			3			19

of which occurs in passerines (e.g., Morton and Young 1986, Otter et al. 2002). Thus, a combination of vocal cues and knowledge of male location should provide some certainty of identifying resident males correctly.

The utility of this technique may be limited for comparing calls between years if males taking over a territory were to converge on the calling patterns of previous residents, with the note structure somehow being linked to location (e.g., possibly to increase transmission in different microhabitats). This seems highly unlikely; however, because the particular call type we measured is already stereotyped among males for maximum transmission through forest habitat and has a sufficiently narrow range of variation between individuals that it would likely be of no benefit for increasing sound transmission. Our data also provided evidence that vocal characteristics were not linked to a particular site, as one of the test sites occupied both years had a classification rate (0%) akin to random. It therefore appears that variation in the advertisement call between males is due to inherent individual differences, thereby providing a useful tool for monitoring.

Recently, some studies have started exploring the technique of vocal individuality to monitor population trends and to learn about site fidelity and territory turnover. For example, Delpont et al. (2002) had great success monitoring individual male and female African Wood Owls (*Strix woodfordii*), determining turnover rates over a 12-yr period and thereby providing opportunities to measure aspects of population turnover along with life history traits. Turnover rates between two years in Common Scops Owls (*Otus scops*) have also been determined using similar analyses to ours (Galeotti and Sacchi 2001). Although our sample is small, the preliminary analysis of site fidelity leads us to believe that this technique may have utility in monitoring the Queen Charlotte Islands' subspecies of Northern Saw-whet Owl. Based on our results, we suggest that there is some level of site fidelity at occupied sites between years, a behavior which although occurring at low rates, is largely uncommon in the *A. a. acadicus* subspecies (Cannings 1993). Our preliminary results with this analysis suggested that further study may be warranted to determine the levels of site fidelity in the *A. a. brooksi* subspecies, given that high site fidelity is often associated with increased reproductive success (Newton 1993) as well as a steady food supply (Löff-

gren et al. 1986). As this subspecies is not migratory, it is less likely to be as nomadic as the *A. a. acadicus* counterpart, and hence, we would expect the breeding behavior to potentially differ in regard to site fidelity. Because a lack of site fidelity is often associated with reproductive failure in the previous year (Bried and Jouvetin 1999), and high breeding success is often associated with high quality habitats, monitoring of levels of site fidelity may give insight into the habitat structure or type that facilitates increased reproductive success.

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LITERATURE CITED

- BIBBY, C.J., N.D. BURGESS, D.A. HILL, AND S.H. MUSTOE. 2000. Bird census techniques, 2nd Ed. Academic Press, San Diego, CA U.S.A.
- BRIED, J. AND P. JOUVETIN. 1999. Influence of breeding success on fidelity in long-lived birds: an experimental study. *J. Avian Biol.* 30:392-398.
- CANNINGS, R.J. 1993. Northern Saw-whet Owl. In A. Poole and F. Gill [Eds.], The birds of North America, No. 42. The Birds of North America, Inc., Philadelphia, PA U.S.A.
- DELPONT, W., A.C. KEMP, AND J.W.H. FERGUSON. 2002. Vocal identification of individual African Wood Owls *Strix woodfordii*: a technique to monitor long-term adult turnover and residency. *Ibis* 144:30-39.
- EAKLE, W.L., R.W. MANNAN, AND T.G. GRUBB. 1989. Identification of individual breeding Bald Eagles by voice analysis. *J. Wildl. Manag.* 52:450-455.
- FOSTER, C.C., E.D. FORSMAN, E.C. MESLOW, G.S. MILLER, J.A. REID, F.F. WAGNER, A.B. CAREY, AND J. LINT. 1992. Survival and reproduction of radio-marked adult Spotted Owls. *J. Wildl. Manag.* 56:91-95.
- GALEOTTI, P., M. PALADIN, AND G. PAVAN. 1993. Individually distinct hooting in male Pygmy Owls *Glaucidium*

- passerinum*: a multivariate approach. *Ornis Scand.* 25: 15–20.
- AND G. PAVAN. 1991. Individual recognition of male Tawny Owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethol. Ecol. Evol.* 3:113–126.
- AND R. SACCHI. 2001. Turnover of territorial Scops Owls *Otus scops* as estimated by spectrographic analyses of male hoots. *J. Avian Biol.* 32:256–262.
- GILBERT, G., P.K. MCGREGOR, AND G. TYLER. 1994. Vocal individuality as a census tool: practical considerations illustrated by a study of two rare species. *J. Field Ornithol.* 65:335–348.
- LÖFGREN, O., B. HÖRNFELD, AND B.G. CARLSSON. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus*) in relation to cyclic food production. *Oecologia* 69:321–326.
- MCGREGOR, P.K. AND P. BYLE. 1992. Individually distinctive bittern booms: potential as a census tool. *Bioacoustics* 4:93–109.
- , T.M. PEAKE, AND G. GILBERT. 2000. Communication behavior and conservation. Pages 261–280 in L.M. Gosling and W.J. Sutherland [EDS.], *Behaviour and conservation*. Cambridge Univ. Press, Cambridge, U.K.
- MORTON, E.S. AND K. YOUNG. 1986. A previously undescribed method of song matching in a species with a single song "type", the Kentucky Warbler (*Oporornis formosus*). *Ethology* 73:334–342.
- NEWTON, I. 1993. Age and site fidelity in female sparrowhawks, *Accipiter nisus*. *Anim. Behav.* 46:161–168.
- OTTER, K. 1996. Individual variation in the advertisement call of male Northern Saw-whet Owls. *J. Field Ornithol.* 67:398–405.
- , L. RATCLIFFE, M. NJEGOVAN, AND J. FOTHERINGHAM. 2002. Importance of frequency and temporal song matching in Black-capped Chickadees: evidence from interactive playback. *Ethology* 108:181–191.
- PEAKE, T.M., P.K. MCGREGOR, K.W. SMITH, G. TYLER, G. GILBERT, AND R.E. GREEN. 1998. Individuality in Corncrake *Crex crex* vocalizations. *Ibis* 140:121–127.
- AND P.K. MCGREGOR. 2001. Corncrake *Crex crex* census estimates: a conservation application of vocal individuality. *An. Biodiv. Conserv.* 24:81–90.
- REEBECK, M., R. CORRICK, B. EAGLESTONE, AND C. STAINTON. 2001. Recognition of individual European Nightjars *Caprimulgus europaeus* from their song. *Ibis* 143:468–475.
- SPECHT, R. 2000. Avisoft SAS Lab Pro version 3.82b. Avisoft Bioacoustics, Berlin, Germany.
- STATSOFT, INC. 2003. STATISTICA version 6. Stat Soft Inc., Tulsa, OK U.S.A.
- TERRY, A.M.R. AND P.K. MCGREGOR. 2002. Census and monitoring based on individually identifiable vocalizations: the role of neural networks. *An. Conserv.* 5: 103–111.
- WILEY, R.H. AND D.G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Academic Press, New York, NY U.S.A.

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